Modelling Regeneration and Recruitment in a Tropical Rainforest

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A two-stage model predicts recruitment of the 100 species which account for 97% of all recruitment observed on 217 permanent sample plots in the tropical rainforest of north Queensland. The first stage predicts the probability of the occurrence of any recruitment from stand basal area and the presence of that species in the existing stand. These probabilities can be implemented stochastically, or deterministically by summing for each species until unity is reached, recruitment initiated and the accumulated probability reset. The second stage indicates the expected amount of recruitment, given that it is known to occur, and employs stand basal area, the relative number of trees of that species in the stand, and site quality. This approach is easily implemented and provides good results.

Introduction

Growth models may neglect the simulation of regeneration because of a lack of data, difficulty of modelling, or because it is considered unnecessary as silviculture involves clearfelling and replanting. However, natural regeneration forms an essential component of selection harvesting systems used in rainforest management, and long term yield forecasts must take account of the presence and amount of this regeneration.

A review of the literature indicates two approaches to predicting regeneration and recruitment. *Regeneration models* predict the development of trees from seed or seedlings. As suitable data for modelling regeneration are difficult to obtain, many models predict recruitment rather than regeneration. *Recruitment models* predict the number of stems reaching or exceeding some specified nominal size limit (e.g. 1.3 m height, 3 m height, 10 cm d.b.h.o.b., etc.). Recruitment models may employ a static approach which predicts a constant amount each year irrespective of stand condition, or may be dynamic and respond to stand condition.

Static approaches to the prediction of recruitment assume that the amount of recruitment observed during the period of data collection reflects the long term average, and that this amount will not vary greatly between projection periods predicted by the model. Such assumptions of static recruitment are common in stand table projection and matrix approaches. Usher's (1966) matrix model for Scots pine predicted recruitment as a static proportion of the number of trees in the larger size classes and thus recruitment increased as stand density increased. More realistic matrix approaches may predict recruitment diminishing with increasing stand density (e.g. Buongiorno and Michie 1980), or only after the death of another tree (e.g. Bosch 1971). Although these approaches are rather empirical, they may provide useful estimates of recruitment for stands which do not differ greatly from the source stands used for model development.

Other approaches attempt to predict the number of stems recruited as a function of stand condition. These vary from the highly empirical to those that model some simple biological hypothesis. Letourneau (1979) used an empirical approach with 33 estimated parameters to predict numbers of stems, and accounted for time between remeasures in estimating size of recruits. Landford and Cunia (1977) predicted total number of recruits (at 4 inches diameter) deterministically, but the size and species stochastically. Both these models used estimates of sapling density (numbers of stems in the 1, 2 and 3 inch d.b.h. size classes) in

their equations and this estimate was assumed to remain constant through time; as saplings were recruited, new regeneration was assumed to take their place. This limits the utility of the model for extrapolating inventory data, as such data (sapling density) may not be recorded during operational inventory.

Hann (1980) predicted recruitment with an exponential function of site index, stand basal area, and basal area in the smallest size class. His simulation cycle was five years, and this ensured a realistic five-year lag in the appearance of recruitment stimulated by the reduction in stand basal area following logging.

Vanclay (1989a) predicted the total amount of recruitment at 20 cm diameter in tropical moist forests in north Queensland as a linear function of stand basal area and site quality. The composition of this recruitment was determined by predicting the proportion in each of five species groups, and standardizing the proportions. The proportion for each species groups was predicted from the stand basal area, the site quality and the basal area of that species group (e.g. for the large, fast-growing species):

$$P_1 = \left(1 + e^{2.407+0.005608BA-0.01105B_1-0.00464B_1SQ}\right)^{-1}$$

where BA is total stand basal area (m^2/ha), B_1 is the basal area of group 1 species (m^2/ha), and SQ is the growth index. These proportions were standardized to ensure they summed to unity: $P'_1 = P_1/\sum P$

Botkin *et al.* (1972) established an ecological approach to modelling recruitment at 0.5 cm diameter on their ten metre square plots. They assumed that a seed source was available for each of the major species considered by their model, and compiled a list of possible species for the plot being modelled, on the basis of shade tolerance, growing season and soil moisture. If the plot leaf area index (LAI) was less than a specified threshold, 60 to 75 cherry trees were recruited on the plot. If the plot LAI exceeded the first threshold, but was less than a second larger threshold, some (0-13) birches were recruited. If the plot LAI exceeded both these thresholds, a random choice of the remaining suitable shade tolerant species was made, and a random number (0, 1 or 2) of each species was recruited. Shugart and West (1977) followed a similar approach, but identified the requirements of each species for mineral soil or leaf litter, introduced stochastic elements of variable weather and animal browsing, and also modelled sprouting from dead trees. They recruited trees when they reached breast height. Similar succession models exist for subtropical rainforest in Australia (Shugart *et al.* 1980) and tropical rainforest in America (Doyle 1981). Reed (1980) followed an approach somewhat similar to Botkin *et al.* (1972), but introduced alternate seed-years and ‘‘off-years’’ and imposed a maximum stocking of 2500 stems per hectare, irrespective of size, above which no

recruitment could occur.

One of the difficulties in modelling recruitment is the great variability in regeneration. Stand condition accounts for some of this variation, periodicity of mast years and prevailing climate accounts for some, but regeneration remains a rather stochastic process, providing difficulties for efficient model estimation. Much of the variability associated with regeneration is due to the fact that during any period some regeneration may or may not occur, and that if the data are partitioned into a two-state system, the ability to predict the amount of regeneration is greatly enhanced. With a two-state approach, the first equation estimates the probability that some regeneration or recruitment will occur, and can be estimated using logistic regression with presence/absence as the dependent variable. The second stage is a conditional function to predict the amount of recruitment, given that some is known to occur, and can be estimated using ordinary linear regression. Hamilton and Brickell (1983) gave an example of such a two-stage approach applied to the prediction of defective volume in standing trees, which can be applied equally well to modelling recruitment.

Stage and Ferguson (1982) and Ferguson *et al.* (1986) used a two-stage approach to predict recruitment in the Prognosis model (Stage 1973, Wykoff *et al.* 1982, Wykoff 1986). They used a stochastic procedure to predict the regeneration on 50 subplots each 1/300 acre (about 0.001 ha), and these data were aggregated into the main Prognosis model at 10 and 20 years after disturbance. They predicted the probability that some regeneration would occur using environmental variables (habitat, slope, aspect, elevation), distance to seed source, residual basal area and time since disturbance. Given that regeneration is known to occur, the expected number of trees is determined using pseudo-random numbers, and determines the number of cohorts for that subplot. The number of species present, and the identity of these species were also stochastically determined. Height of regeneration is deterministically predicted. The model considers three categories of regeneration: ‘‘best’’ trees comprising the tallest two trees per plot regardless of species, the tallest tree of each additional species present, and the tallest four of any remaining trees. Best trees were assumed to be advance growth of shade tolerant species if established three years prior to disturbance. Regeneration within each category was predicted independently, and differed considerably in composition (e.g. advance growth was more likely to comprise shade tolerant species).

Some models simulate the growth of trees from seedlings to breast height within a separate ‘‘regeneration model’’ or ‘‘understory operation’’ (Ek and Monserud 1974a,b, Dudek and Ek 1980). The approach is

sufficiently flexible that almost any size may be used as the criterion for recruitment into the main stand. Ek and Brodie (1975) simulated only suckers developing after logging (predicted from stand basal area before and after logging, site index and treatment), but many models simulate the development of regeneration throughout the development of the stand. Modelling may start at any of a number of stages. Leak (1968) modelled regeneration from the stage of flower development, Ek and Monserud (1974a,b) from seed fall. Germination could equally well be considered, and Vanclay (1988) started with ''establishment'' when the seedling has survived its first year after germination. An advantage of the approach is that it realistically models the time taken for regeneration to be recruited following a reduction in stand density due to logging. Recruitment models which employ an expression of stand density may lead to overestimates of recruitment in the projection period immediately following logging.

Vanclay (1988) predicted the amount of established one-year-old regeneration in *Callitris* forest from stand basal area and site quality. Regeneration was modelled as cohorts representing height classes until it reached breast height, when it was recruited to the main model. A maximum of ten cohorts were employed. Under ideal conditions (good sites with low stocking), these cohorts represented annual flushes of regeneration. Where regeneration exhibited slower growth and took more than ten years to reach breast height, the most similar cohorts were amalgamated to ensure that the limit of ten cohorts was not exceeded.

Ek and Monserud (1974a,b) adopted a more detailed approach to predict recruitment into their stochastic distance-dependent individual tree model. The regeneration model used cohorts representing the number of stems for each species and age in a number of subplots within the main plot being simulated. A Monte Carlo approach selected good, moderate and poor seed years according to the observed frequency for each species. Seed and sprout production were estimated for each overstorey tree as a function of its size and the threshold age, and were distributed across the subplots according to the parent tree's position, height and crown width. Germination was predicted as a stochastic function of microsite and canopy cover conditions. Each year, a germinant or tree in the understorey may die, or survive and attain some height increment (function of cover, species and age). When tree height reached breast height it was recruited into the main model. If a tree did not attain this height within a specified time (e.g. 25 years for black spruce), it died.

Monserud and Ek (1977) refined this approach, improving the efficiency by reducing the number of cohorts to be modelled. They assumed that understorey tree size was more relevant than tree age, and modelled the development of trees to 7.6 metres height using five height cohorts of varying size, using the movement

ratio approach (see section 6.2). The height increment of the mean tree was predicted from the potential height increment (a function of height and site), overstorey competition index (a relative size-distance index), shade tolerance (a function of species and height), and stand density. Monserud and Ek determined that five cohorts were required to model the understorey without compromising accuracy. Such detailed approaches (Ek and Monserud 1974a,b, Monserud and Ek 1977) may not be warranted for yield prediction models, but may be relevant for models for analysing silvicultural alternatives for intensively managed stands.

One difficulty with regeneration models is ensuring compatibility with inventory data when the model is used for yield prediction. Inventory data frequently sample only the larger stems (e.g. ≥10 cm d.b.h.), and smaller stems may remain unsampled. Thus there may be some censorship of data. Such problems are more common for regeneration models (which predict regeneration at very small sizes) than for recruitment models which predict recruits at larger diameters (e.g. 10 cm). To avoid this censorship, it is necessary either for inventory to provide a count of the smaller stems, or for a model to predict the likely incidence of such stems from overstorey stocking. Augmenting such censored data with an ''average'' small tree distribution for the forest type is preferable to using the unadjusted censored data (Randall *et al.* 1988).

Difficulties in obtaining uncensored data during operational inventory limit the utility of regeneration models for yield forecasting. Data concerning regeneration are often not available, or may be unreliable due to inability to reliably identify species of seedlings, whereas recruitment data are always available from permanent sample plots. The germination and initial survival of seedlings in the rainforest is an uncertain phenomenon; vast numbers of individuals and species may germinate but never attain a significant size. The longer term survival and continued growth of these seedlings is much more under environmental control and thus recruitment is more predictable than regeneration. Thus modelling recruitment at some nominal size provides a viable alternative.

Data

The present study concerns the tropical rainforests of north-east Queensland. These forests have been managed for conservation and timber production for more than eighty years (Just 1991), and prior to their recent inclusion on the World Heritage List, provided a sustained yield of veneer and sawlogs of 60 000 cubic metres per annum (Preston and Vanclay 1988). The Queensland Department of Forestry (1983) research programme provided a database of 250 permanent sample plots with a measurement history of up

to forty years. These plots range in size from 0.04 to 0.5 hectares, and have been regularly re-measured (Vanclay 1990). All trees exceeding 10 cm dbh (diameter over bark at breast height (1.3 m) or above buttressing) were numbered, tagged and measured for diameter. The plots sample virgin, logged and silviculturally treated forests.

Pairs of consecutive remeasurements (i.e. all non-overlapping intervals) were selected from the database and formatted to provide a data file suitable for input to the statistical package GLIM (Payne 1986). Site quality (Vanclay 1989b) could not be estimated for some plots and the omission of these plots left 217 plots for the present study. Thus the data file used for these analyses contained 791 observations of on the incidence and amount of recruitment (at 10 cm dbh) for each species. The file also contained details of stand and site variables such as stand basal area, site quality and soil type.

Species identity is recorded in the database as a three character mnemonic (the Forest Research Branch code) for the great majority of species, but a few trees of indeterminate identity were identified only as miscellaneous. However, correct species identification is often difficult in these forests, and routine resource inventory procedures record only the standard trade name (Standards Association of Australia 1983), using a subset of the mnemonics known as the Harvesting and Marketing (H&M) code. Although the H&M code retains the correct identity of most species, several members of a genus may share a common code, as may members of more than one genus with similar timber characteristics. There are also additional non-commercial species simply labelled miscellaneous. As the present study was to develop a recruitment model for operational yield prediction purposes (e.g. Vanclay and Preston 1989), it was appropriate to use the H&M codes. Three hundred of the FRB codes in the data were converted into 238 H&M codes for analysis, and the remaining one hundred with no H&M equivalent were grouped as miscellaneous.

Method

The recruitment data suggest an excessively heteroscedastic distribution, until partitioned for the two-stage modelling approach. Given that recruitment is known to occur, estimation of the amount of recruitment is possible with ordinary least squares multiple linear regression. The probability that any recruitment occurs can be estimated with a logistic equation fitted using maximum likelihood estimation techniques. Thus recruitment can be predicted using a two-stage model, with one equation to predict the probability that any recruitment of a given species occurs, and another to predict the amount, given that recruitment is known to

occur.

Number of species to model

Of the 239 H&M codes occurring on the permanent sample plots, 213 of these were observed to occur as recruitment on one or more occasions. However, the contribution of individual species to the total recruitment varied greatly. Sixty species accounted for 90% of all recruitment, 80 species for 95%, and 100 species accounted for 97% of all recruitment observed (Figure 1). The remaining 3% of recruitment comprised 113 species, all of which offered insuffi cient data for meaningful analyses of regeneration characteristics. Accordingly, only the more prevalent 100 species were included in the recruitment model. These species were those which were observed as recruitment on nine or more occasions, included a reasonable number of species of both commercial and non-commercial, light-demanding and shade tolerant species, and should provide a reasonable representation of the forest. Simulating the recruitment of these 100 species should provide suffi cient precision for yield prediction purposes, provided that simulated ecological consequences are interpreted carefully.

Two options exist for recruitment of the remaining 113 species: they may be aggregated with the miscellaneous group, or may be ignored. Both options have disadvantages. The less abundant species may have ecological characteristics unlike those dominating the miscellaneous group, and aggregating these could lead to bias. Similarly, ignoring this recruitment also leads to bias. In the present study, they were ignored since they comprise such a small component of the total recruitment.

Aggregating Species

It is impractical to develop recruitment models for each of these 100 individual tree species, because of the large number of functions that would be required, and because of the paucity of data for many species inhibits the development of reliable relationships. Thus for effi cient estimation of recruitment, it is desirable to aggregate these species into several groups. This reduces the number of functions required to a more manageable number, and avoids the requirement for specifi c equations for species with few data. Such groupings need not form the basis for growth modelling, as simulation models can retain the individual identity of all species (Vanclay and Preston 1989), but are necessary for the estimation of increment, mortality and recruitment functions. Ideally, species should be grouped on *a priori* grounds, and tests performed to justify the validity of such groupings. This may be possible in temperate forests where

there are few species with well documented ecological characteristics, but is unrealistic for the 100 species in the present study. Taxonomy (family or genus) may not provide a good guide to the regeneration strategy and other methods based on successional status, seed morphology, etc. may be rather subjective. Regeneration is dependent upon stand density and other factors, so a grouping based on average recruitment may be specific to the data set used. Not only is it difficult to resolve which species to combine, but it is not clear how many groups are required.

Meldahl *et al.* (1985), Leech *et al.* (1991) and Vanclay (1991a,b) have examined procedures to resolve these questions. Meldahl *et al.* (1985) argued that the grouping should reflect the dynamics of growth, and this could be best expressed through the coefficients of a regression equation on diameter increment. They attempted cluster analysis on these coefficients, but found that reasonable results could be obtained only when the regression analysis was constrained to a single explanatory variable. Their best results were obtained using the basal area of trees larger than the current tree as the explanatory variable. Cluster analysis was weighted by the inverse of the significance level of slope parameter, and provided twenty clusters from 110 species-type equations. The number of data assigned to each cluster varied greatly, and the outcome was subjectively adjusted to provide the final grouping. The adequacy of final groups was tested by fitting a multiparameter linear function and examining the total (across clusters) residual sums of squares, on the assumption that a better grouping would result in a better fit. Whilst the method provided a grouping of similar elements, it did not provide a unique solution.

Leech *et al.* (1991) used a Behrens-Fisher analogue of Hotelling's T^2 to group 27 species for volume equation estimation. They used a polynomial equation to predict tree volume (V) from tree diameter (D) for tree i:

$$V_i = \beta_{0i} + \beta_{1i} D + \beta_{2i} D^2 + \cdots + \beta_{ni} D^n$$

Then, representing the vector of coefficients as

$$u'_i = [\beta_{0i}, \beta_{1i}, \beta_{2i}, \cdots \beta_{ni}],$$

Hotelling's T^2 between two species i and j can be defined as

$$d_{ij}{}^2 = (u_i - u_j)' S^{-1} (u_i - u_j)$$

where S^{-1} is the combined covariance matrix of regression coefficients for species i and j. By calculating all possible combinations a symmetric matrix with zero diagonal elements can be formed. Principal coordinate analysis (Gower 1966) was used to group species on the basis of this matrix. Leech *et al.* (1991)

concluded that the technique should only be used when the order of the polynomial and the sign of the highest term were the same for each of the two individual species equations. The method was also computationally intensive.

Vanclay (1991a) devised an objective means to aggregate 237 species into 41 groups to enable efficient estimation of diameter increment functions for a growth model of tropical rainforest in north Queensland. His approach involved:

- Ranking species in order of increasing number of observations.
- Assigning the species of highest rank the founding species of group 1.
- For each species in decreasing order of rank, conducting pairwise F-tests with all founding species of higher rank. If the incoming species was significantly different ($p<0.01$) from all existing founding species, it became the founding species of a new group. Species not significantly different from all founding species remained ungrouped.
- After identifying all founding species, those species remaining ungrouped were compared, in order of rank, with all existing groups, and grouped with the most similar group. Similarity was determined as that grouping which lead to the smallest increase in residual sum squares when the incoming species was amalgamated with the group. These comparisons were made with the whole group, not just the founding species.

This approach overcomes many of the difficulties associated with the alternatives discussed above, and is computationally efficient. Instead of a comparison of all possible pairs, initial comparisons are made between species with many data, reliable parameter estimates and homogeneous variance. Species with few data are only later compared with one of these major groups. It also avoids Leech's *et al.* (1991) need to arbitrarily select a subset of the more numerous species to define the groups. This selection is by no means intuitive as in Vanclay's (1991a) study the species ranked 186 with only 13 observations initiated a new group. This approach provided an objective basis for aggregating species, but there is, unfortunately, no guarantee that the outcome is optimal. However, it provided an efficient, objective and repeatable means to combine many species into a manageable number of groups for modelling the diameter increment of tropical rainforests. Vanclay (1991b) also used a variation on this approach to aggregate species to predict mortality using logistic equations fitted by maximum likelihood estimation and compared using the

likelihood ratio test.

Explanatory Variables

Because the model is to be used for projecting operational inventory data for yield predictions, all driving variables should be readily obtainable in routine resource assessment. Basic stand variables such as site quality and stand basal area are obvious candidates for explanatory variables. The presence of the species in the existing stand should also be an important variable. However, it is not necessary that a species exist in or near a stand for regeneration to occur. Many rainforest species have efficient means of dispersal (Stocker 1983), and occurrence in the immediate vicinity is not a prerequisite for regeneration of all species. Stand basal area and the presence or relative abundance of the species were used to aggregate species into groups, but additional variables were considered for the final group equations.

Many of the plots used in the present study were logged or silviculturally treated, and the time since such disturbance may provide a useful explanatory variable. Analyses indicated that time since last logged explained little of the variation observed in the data, but that time since the last silvicultural treatment offered greater potential. Unfortunately, time since treatment was highly correlated with stand basal area and both variables could not be used in fitting models to the data without causing instability in the estimated parameters. Stand basal area was preferred as an explanatory variable, particularly as silvicultural treatment was applied mainly in experiments and few areas were treated operationally.

Other species were also screened as possible indicators of favourable or unfavourable conditions for recruitment. Such species need not have a direct antagonistic or synergistic effect on the developing regeneration, but may merely indicate suitable stand conditions not reflected in the basic stand variables. Candidates for such indicator species were selected both subjectively using ecological principles, and empirically using an comprehensive screening process. Subjective selection identified groups of species indicative of environmental conditions. Thus palms were chosen as indicators of moist sites and sclerophyllous species (*Acacia*, *Casuarina*, *Eucalyptus*, *Melaleuca* spp.) were chosen as indicative of marginal rainforest sites. Other species including *Agathis* species, *Backhousia bancroftii* and *Blepharocarya involucrigera* may dominate some rainforest stands and were also considered as potential indicator species.

Empirical screening of species for possible indicators involved the compilation of a correlation matrix for

all species in the data, showing the correlation between occurrence in the existing stand and occurrence of recruitment. The amount of recruitment was not considered as, given that recruitment is known to occur, the amount is determined largely by stand basal area and site quality, and additional variables contribute little more to the model. The correlation matrix indicated a large number of species pairs with significant correlations. Twenty five species, some having the greatest number of significant entries, and some the highest correlations, were selected for further screening using regression analysis. Many of these species were highly correlated with basic stand variables (e.g. pioneer and gap colonizing species indicate low basal area), and were not significant when included in regression analyses with stand variables such as stand basal area and site quality. Eight species were found to be significant in two or more logistic regressions of recruitment occurrence on basal area, site quality and species occurrence, and these were used as indicator species in further analyses.

Results

Probability of Recruitment

Preliminary analyses for several species with many data suggested that most of the variation in occurrence could be explained by stand basal area, and the presence or absence of that species in the stand. Thus these two variables were used as explanatory variables in comparing species for aggregation. Comparisons used Vanclay's (1991b) method (pairwise likelihood ratio tests ~ χ^2) and the model:

$$P = \left(1 + e^{-(\beta_0 + \beta_1 PRES + \beta_2 BA)}\right)^{-1}$$

where P is the annual probability of recruitment for that species, BA is stand basal area (all stems 10+ cm d.b.h.) and $PRES$ is a binary (0,1) variable indicating the presence (1) or absence (0) of that species in the (10+ cm d.b.h) stand. The data were weighted by the inverse of the time interval to account for the differing re-measurement frequency.

This analysis indicated five groups (Appendix), based on pairwise comparisons of the equation fitted to the 791 observations on each of 100 species. Of these 79100 observations, a total of 4586 confirmed the presence of recruitment for the particular species. Following grouping, the inclusion of additional explanatory variables was investigated. Soil parent material, time since treatment and the logarithm of stand basal area were found to be significant. Thus the final equation was

$$P = \left(1 + e^{-(\beta_0+\beta_1 PRES+\beta_2 BA+\beta_3 Log(BA)+\beta_4 TR+\beta_5 SOIL)}\right)^{-1} \quad [1]$$

where P, BA and $PRES$ are as defined above, and TR is the treatment response ($TR = te^{t/9}$ where t is years since last silvicultural treatment), and $SOIL$ is a binary variable which takes the value 1 on soils derived from basic volcanic and coarse granite parent materials, and zero otherwise. The treatment response term (TR) provides for a maximum response nine years after silvicultural treatment. The analysis was weighted by the inverse of the time interval to account for the differing re-measurement intervals and provide annual probabilities of recruitment.

Some of the parameter estimates in Table 1 are not significant at the usual levels of significance, but have been retained in the model provided that the sign and magnitude of the estimate is consistent with parameters for other species groups, and that parameter estimates for at least one species group were significant at the usual levels. The parameter estimates for $\beta_3 Log(BA)$ were associated with large standard error estimates, but collectively were significant (likelihood ratio test statistic $\chi^2 = 14$ on 5 d.f., $P = 0.016$), and provided a more realistic response. The inclusion in the model of both the terms BA and $Log(BA)$ ensures a low probability of recruitment for low stand basal area consistent with the available data (Table 3), and predicts a maxima within the range of the data used in the present study (Figure 2).

Amount of Recruitment

A subset of the database comprising 4586 records provided estimates of the amount of recruitment given that it was known to occur. Preliminary analyses of the more abundant species indicated that stand basal area and relative abundance of the species in the (10+ cm d.b.h.) stand explained most of the variation. The curvilinear response provided by the logarithmic transformation of relative abundance gave a slightly better fit than a linear model, and ensured more conservative extrapolations for the several species for which the present data spanned only a small part of the possible range of values. Species were aggregated using Vanclay's (1991a) methodology (pairwise F-tests) and the equation:

$$Log(N) = \beta_0 + \beta_1 Log(BA) + \beta_2 Log(RNO + 0.2) \quad [2]$$

where N is the number (trees/ha/yr) of recruits (at 10 cm d.b.h.), BA is the stand basal area (m^2/ha) and RNO is the relative number ($0 \le RNO \le 1$) of that species in the (10+cm d.b.h.) stand.

This analysis indicated eight species groups. Following grouping, the inclusion of additional explanatory variables was investigated. Site quality and soil type were significant, and the final model was:

$$Log(N) = \beta_0 + \beta_1 Log(BA) + \beta_2 Log(RNO + 0.2) + \beta_3 SQ + \beta_4 SOIL$$

where N, BA and RNO are as previously defined, SQ is site quality estimated using Vanclay's (1989b) growth index, and $SOIL$ is a binary (0,1) variable which takes the value 1 on alluvial and fine-grained (''Tully'') granite soils and zero elsewhere. Parameter estimates are given in Table 2 and the relationship is illustrated in Figure 2. No indicator species contributed significantly to this relationship. Some parameters in Table 2 are not statistically significant (i.e. P>0.05), but were retained in the model provided that the corresponding term was significant (P<0.001) for other species groups, and that the sign and magnitude of the parameter estimate were logical and comparable to those of other groups.

Analysis of the present data has been complicated by the different plot sizes and re-measurement intervals. To provide a consistent basis for analysis, probabilities of recruitment have been adjusted to annual probabilities by weighting by the inverse of measure interval, and amounts of recruitment have been standardized to stems/hectare/annum. However, this results in a double correction which underestimates the expected recruitment. Thus the parameters β_0 in Table 2 have been adjusted to provide unbiased estimates of recruitment (Table 3). Figure 3 illustrates these relationships.

Discussion

Checking Predictions

One of the best ways to gauge the quality of a model is to compare model predictions with raw data; both with the data used in fitting the model and with independent data. Such comparisons are especially important in multi-stage models such as the present one. Table 3 contrasts predictions with the raw data used in fitting the model. Comparisons with independent data will be made in another paper.

Table 3 indicates the total recruitment observed (stems/ha) (O) and the recruitment predicted by the model (P) (i.e. Probability × Amount × Years). There is generally a good correspondence, except for two cells. Species group 2-2 with 80 sq m/ha basal area indicates a big discrepancy due to the recruitment of 731 stems/hectare on one plot (0.04 ha) during a single interval (5.8 years). Although anomalous, there seemed no good reason to reject this datum. Another discrepancy occurred for species group 2-5 with 4 sq m/ha basal area for which large amounts of recruitment were predicted but none were observed on a single plot over two consecutive time periods. This discrepancy occurred for an enrichment planting study in which natural regeneration was cut to enhance the growth of the planted trees (not included in the present data). The predictions give a reasonable indication of the recruitment which might have eventuated in the absence

of this treatment. Since no recruitment was observed, these two data were used only in fitting the model for probability of recruitment, and not in fitting the model for amount of recruitment. Apart from these two major discrepancies, predictions seemed reasonable (Table 3 & Figure 4).

Correlation of groupings

This study has employed two independent grouping strategies. Table 4 demonstrates that this was in fact necessary. There is no evidence of any correlation between the two groupings (Expected non-empty cells=25, actual=22, $\chi^2_4 = 4.23$, P=0.4). ''Founding'' species which are significantly different are indicated in Table 4 which cannot be collapsed without amalgamating some of these species into a single group. Similarly, there is no evidence that the groupings for the prediction of diameter increment (Vanclay 1991a) or for mortality (Vanclay 1991b) are indicative of recruitment pattern.

Implementation

Application of the model requires an estimate of the presence and relative abundance of each species in the stand. This poses no problem for short term predictions, but offers two alternatives for long term simulations. Should the presence and abundance relate to the composition of the original inventory data, or to the current composition of the simulated stand? Composition of natural stands may vary considerably over time. Flushes of pioneer species following disturbance may be short-lived, and the turnover-rate of species may be high even in undisturbed stands (e.g. Poore 1968). However, it is impossible that predicted recruitment would always be correct, and using simulated composition could further bias predictions. Conversely, if inventory were collected soon after disturbance, they may include some pioneer species which would not be expected to persist long in the stand. Thus the best compromise may be to use the relative abundance of species in the original stand, conditional that the species remains in the simulated stand. This solution is intuitive, cautious and seems to give good results.

Conclusion

The two-stage approach is suited to modelling recruitment of the many species in the tropical forests of north Queensland. The first stage predicts the probability of the occurrence of any recruitment from stand basal area and the presence of that species in the existing stand. These probabilities can be implemented stochastically, or deterministically by summing for each species until unity is reached, recruitment initiated and the accumulated probability reset. The second stage indicates the expected amount of recruitment,

given that it is known to occur, and employs stand basal area, the relative number of trees of that species in the stand, and site quality. This approach is easily implemented and provides good results.

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Appendix

The following list indicates the affinities of species included in the present study. The list indicates the H&M code, botanical and common names, and the group to which the species has been assigned for the prediction of probability and amount of recruitment. A dagger (†) following the group identity indicates that the species was the founding species for the group. The amount of data used in the present study is also indicated, both as the number of occasions on which recruitment was recorded, and the total amount of recruitment observed on all occasions (stems/ha). Some species are denoted with a dash (—) which indicates that the species shares the same H&M code as another species, and data for the two species has been amalgamated.

The species groups reflect similarity of recruitment patterns, and do not necessarily have any other ecological significance. The group numbering reflects the amount of data available for the founding species of the group, and in no way implies any commercial or silvicultural preference. In the interests of brevity, some varieties and subspecies have been omitted from this list. The species presented are those actually represented in the data. Some H&M codes are also applied to other species not present in the database.

H&M Code	Botanical Name	Common Name	Probability Group	Amount Group	No of Observations	Total Recruitment
ALB	*Prunus turneriana*	almondbark	2	5	74	789.9
BBN	*Castanospermum australe*	black bean	4	7	25	583.7
BKR	*Commersonia bartramia*	brown kurrajong	4	4	9	86.3
BLA	*Sloanea australis ssp. parviflora*	blush alder	4	8	33	229.6
BLC	*Planchonella xerocarpa*	blush coondoo	4	8	12	54.4
BLO	*Bleasdalea bleasdalei*	blush silky oak	4	8	26	209.2
BLO	*Opisthiolepis heterophylla*	blush silky oak	4	8	—	—
BLW	*Beilschmiedia obtusifolia*	blush walnut	4	8	23	119.9
BLW	*Endiandra* sp. (RFK 19)	blush walnut	4	8	—	—
BOC	*Brackenridgea nitida ssp. australiana*	brown ochna	4	8	23	148.8
BRC	*Canarium baileyanum*	brown cudgerie	4	8	20	113.4
BRO	*Darlingia darlingiana*	brown silky oak	3	8	97	992.3
BRP	*Podocarpus elatus*	brown pine	4	8	11	71.2
BRP	*Podocarpus grayi*	brown pine	4	8	—	—
BRQ	*Elaeocarpus coorangooloo*	brown quandong	4	8	23	116.8
BRQ	*Elaeocarpus ruminatus*	brown quandong	4	8	—	—
BRT	*Argyrodendron polyandrum*	brown tulip oak	5	4	98	1684.8
BRT	*Argyrodendron trifoliolatum*	brown tulip oak	5	4	—	—
BRY	*Brombya platynema*	brombya	5†	8	17	128.8
BSH	*Syzygium cormiflorum*	bumpy satinash	4	2	16	93.0
BSL	*Acacia aulacocarpa*	brown salwood	2	3	93	3600.4
BSO	*Musgravea heterophylla*	briar silky oak	3	8	54	763.3
BTD	*Glochidion ferdinandi*	buttonwood	4	2	12	81.0
BTD	*Glochidion harveyanum*	buttonwood	4	2	—	—
BTD	*Glochidion sumatranum*	buttonwood	4	2	—	—
BTM	*Castanospora alphandii*	brown tamarind	5	7†	39	1232.2
BUA	*Apodytes brachystylis*	buff alder	5	8	47	324.4
BWD	*Litsea bindoniana*	bollywood	2	5	166	2544.6
BWD	*Litsea leefeana*	bollywood	2	5	—	—
CHS	*Syzygium luehmannii*	cherry satinash	4	8	13	74.6
CLL	*Cryptocarya cinnamomifolia*	cinnamon laurel	4	2	18	185.9
CLO	*Carnarvonia araliifolia*	Caledonian oak	3	4	54	607.7

CMH	*Alangium villosum*	canary muskheart	3	1	35	387.9
CNN	*Aleurites moluccana*	candlenut	5	1	67	999.5
COL	*Cryptocarya* sp. (RFK 2153)	coconut laurel	4	2	12	74.6
COW	*Endiandra dichrophylla*	coach walnut	4	8	30	186.8
COW	*Endiandra montana*	coach walnut	4	8	—	—
COW	*Endiandra tooram*	coach walnut	4	8	—	—
EUQ	*Elaeocarpus eumundi*	Eumundi quandong	4	8	12	95.3
EVD	*Euodia elleryana*	evodia	3	1	36	412.5
FIG	*Ficus spp.*	fi gwood	4	8	28	212.4
FKJ	*Brachychiton acerifolius*	flame kurrajong	4	2	20	154.9
GCB	*Sloanea macbrydei*	grey carabeen	4	8	21	178.3
HKA	*Flindersia iffl aiana*	hickory ash	4	2	22	329.6
HMW	*Alstonia muellerana*	hard milkwood	2	6	121	2606.6
HYW	*Endiandra pubens*	hairy walnut	4	4	9	128.7
IBS	*Polyscias australiana*	ivory basswood	4	4	33	230.6
ILL	*Cryptocarya angulata*	ivory laurel	4	8	17	96.2
KML	*Mallotus mollissimus*	kamala	4	8	75	581.0
KML	*Mallotus philippensis*	kamala	4	8	—	—
KML	*Mallotus polyadenos*	kamala	4	8	—	—
KML	*Rockinghamia angustifolia*	kamala	4	8	—	—
KRS	*Syzygium kuranda*	Kuranda satinash	4	8	62	602.4
LAN	*Acronychia acidula*	lemon aspen	4	5	62	1028.5
MCB	*Xanthophyllum octandrum*	Macintyre's boxwood	4	8	28	179.7
MIS	*Miscellaneous*	Miscellaneous	1†	1†	474	3132.4
MSW	*Flindersia pimenteliana*	maple silkwood	2†	2†	233	12780.7
MWN	*Endiandra sp. aff. E. muelleri*	rose walnut	4	8	28	210.4
NBD	*Omalanthus populifolius*	native bleedingheart	3	1	28	552.7
NEV	*Euodia vitifl ora*	northern evodia	3	8	44	339.6
NHQ	*Elaeocarpus sericopetalus*	hard quandong	4	1	30	317.4
NKP	*Agathis atropurpurea*	Queensland kauri pine	4	8	31	247.5
NKP	*Agathis robusta*	Queensland kauri pine	4	8	—	—
NLL	*Cryptocarya hypospodia*	northern laurel	4	8	22	120.5
NRA	*Alphitonia whitei*	red ash	2	3†	164	3528.1
NRW	*Endiandra cowleyana*	rose walnut	4†	8	42	233.3
NRW	*Endiandra hypotephra*	rose walnut	4	8	—	—
NSB	*Citronella smythii*	silky beech	4	8	26	169.0
NSO	*Cardwellia sublimis*	northern silky oak	3†	4†	150	1557.2
NSS	*Daphnandra repandula*	sassafras	5	4	156	1774.6
NSS	*Doryphora aromatica*	sassafras	5	4	—	—
NTG	*Myristica insipida*	nutmeg	4	8	33	176.8
NTQ	*Elaeocarpus foveolatus*	northern quandong	3	1	24	352.7
PAL	*Gillbeea adenopetala*	pink alder	4	2	21	160.6
PKA	*Alphitonia petriei*	pink ash	2	6	93	2170.5
PLM	*Archontophoenix alexandrae*	piccabeen palm	4	8	11	85.8
PLM	*Licuala ramsayi*	fan palm	4	8	—	—
PPW	*Cinnamomum laubatii*	pepperwood	3	8	27	183.1
PTM	*Jagera discolor*	pink tamarind	4	4	61	670.0
PTM	*Jagera pseudorhus*	pink tamarind	4	4	—	—
PTM	*Sarcotoechia lanceolata*	pink tamarind	4	4	—	—
PTM	*Toechima erythrocarpum*	pink tamarind	4	4	—	—
QMP	*Flindersia brayleyana*	Queensland maple	2	5†	136	2722.4
QSA	*Flindersia bourjotiana*	silver ash	2	5	229	4117.5
QWN	*Endiandra palmerstonii*	Queensland walnut	4	2	9	45.4
RAL	*Caldcluvia australiensis*	rose alder	4	8	11	68.8
RBN	*Blepharocarya involucrigera*	rose butternut	4	8†	29	261.8
RCD	*Toona australis*	red cedar	4	4	44	1009.2
RDT	*Argyrodendron peralatum*	red tulip oak	5	4	91	2109.2
RDT	*Argyrodendron* sp. (RFK 2139)	red tulip oak	5	4	—	—
RLL	*Cryptocarya mackinnoniana*	rusty laurel	4	2	66	479.5
RMP	*Cryptocarya rigida*	rose maple	4	8	10	63.5
ROO	*Darlingia ferruginea*	rose silky oak	3	5	27	303.9
ROO	*Placospermum coriaceum*	rose silky oak	3	5	—	—
RPS	*Syzygium endophloium*	rolypoly satinash	4	8	19	107.4
RSS	*Syzygium johnsonii*	rose satinash	4	2	12	71.1
SBN	*Archidendron vaillantii*	salmon bean	4	8	11	70.5
SBS	*Polyscias elegans*	silver basswood	4	8	68	873.1
SHT	*Halfordia scleroxyla*	saffronheart	4	8	15	102.3
SLQ	*Elaeocarpus grandis*	silver quandong	3	2	62	928.0
SMP	*Flindersia laevicarpa*	scented maple	4	5	10	126.1
SNW	*Endiandra sankeyana*	Sankey's walnut	4	8	12	84.3
SST	*Dendrocnide photinophylla*	shining-leaved stingingtree	3	1	48	693.8

SSW	*Flindersia acuminata*	silver silkwood	3	8	44	463.6
STP	*Canarium australianum*	scrub turpentine	4	8	10	69.7
STP	*Canarium muelleri*	scrub turpentine	4	8	—	—
STS	*Ceratopetalum succirubrum*	satin sycamore	4	8	46	358.4
SVB	*Casearia dallachii*	silver birch	4	7	11	144.9
SYN	*Synima cordierorum*	synima	4	8	17	106.1
TBH	*Tetrasynandra laxiflora*	tetra beech	4	2	18	138.8
TBH	*Tetrasynandra pubescens*	tetra beech	4	2	—	—
TRQ	*Elaeocarpus largiflorens*	tropical quandong	3	8	57	515.0
TST	*Franciscodendron laurifolium*	tulip sterculia	4	8	58	486.8
TYW	*Zanthoxylum veneficum*	thorny yellowwood	5	7	53	830.0
WAL	*Polyosma alangiacea*	white alder	4	3	13	186.6
WAS	*Acronychia acronychioides*	white aspen	5	2	55	492.6
WAS	*Acronychia vestita*	white aspen	5	2	—	—
WBH	*Gmelina fasciculiflora*	white beech	4	2	11	52.8
WBS	*Polyscias murrayi*	white basswood	2	6†	95	2217.2
WCB	*Sloanea langii*	white carabeen	3	8	60	506.3
WCD	*Melia azedarach var. australasica*	white cedar	5	7	17	726.4
WHO	*Stenocarpus sinuatus*	white silky oak	4	8	10	70.0
WHZ	*Symplocos cochinchinensis*	white hazelwood	4	2	34	306.5
YEV	*Euodia bonwickii*	yellow evodia	4	2	41	479.9
YEV	*Euodia xanthoxyloides*	yellow evodia	4	2	—	—
YWN	*Beilschmiedia bancroftii*	yellow walnut	4	8	13	67.6

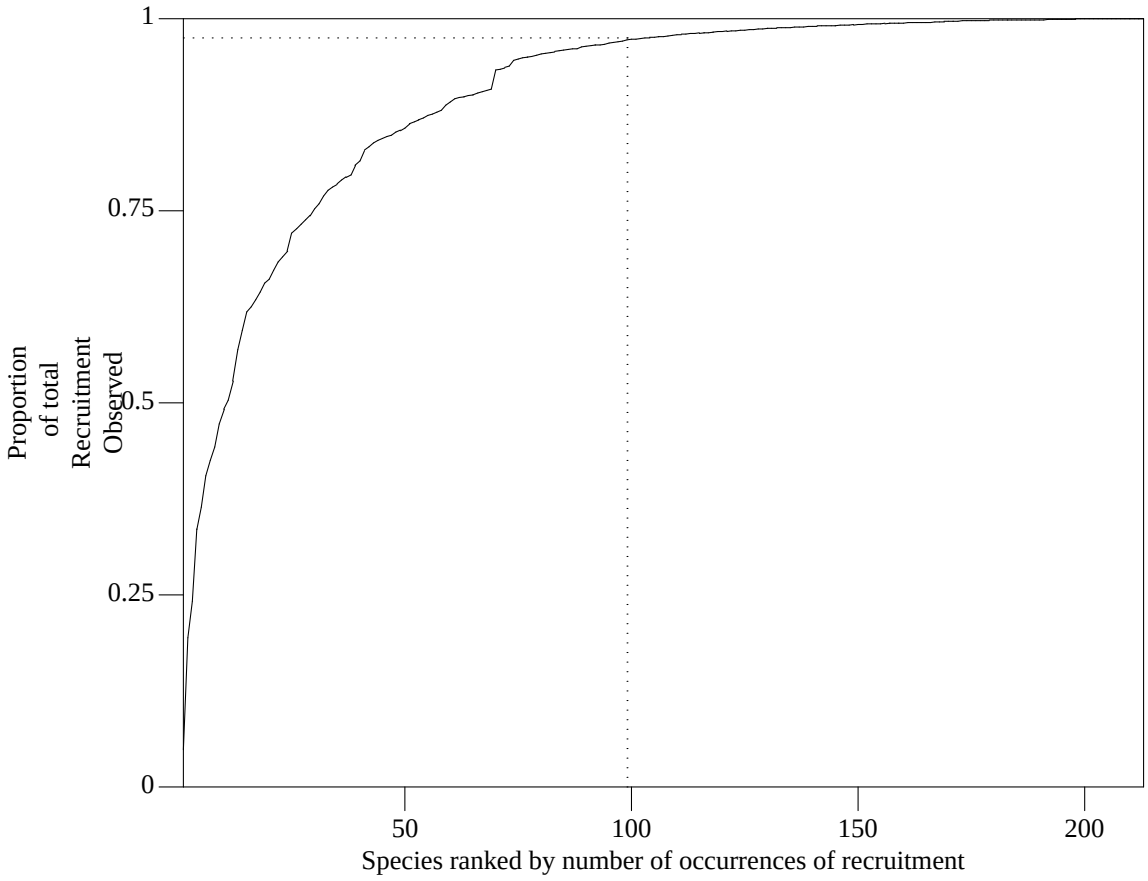

Figure 1. Species composition of Recruitment

TABLE 1. Parameter Estimates for Equation 1

Species Group	Estimate for Parameter					
	β_0	β_1 PRES	β_2 BA	β_3 Log(BA)	β_5 SOIL	β_5 TR
1	–6.769***	1.896***	–0.02784	1.1570	0.2073***	0.2188***
2	–4.726***	2.289***	–0.04703***	0.3960	0.2073†	0.2188†
3	–6.075***	2.491***	–0.06977***	0.6880	0.2073†	0.2188†
4	–8.476***	2.808***	–0.03024**	0.8707**	0.2073†	0.2188†
5	–6.881***	3.782***	–0.03031	0.5213	0.2073†	0.2188†

†These parameters are all identical to $\beta_{4,1}$ and $\beta_{5,1}$
*** indicates P<0.001, ** P<0.01, * P<0.05

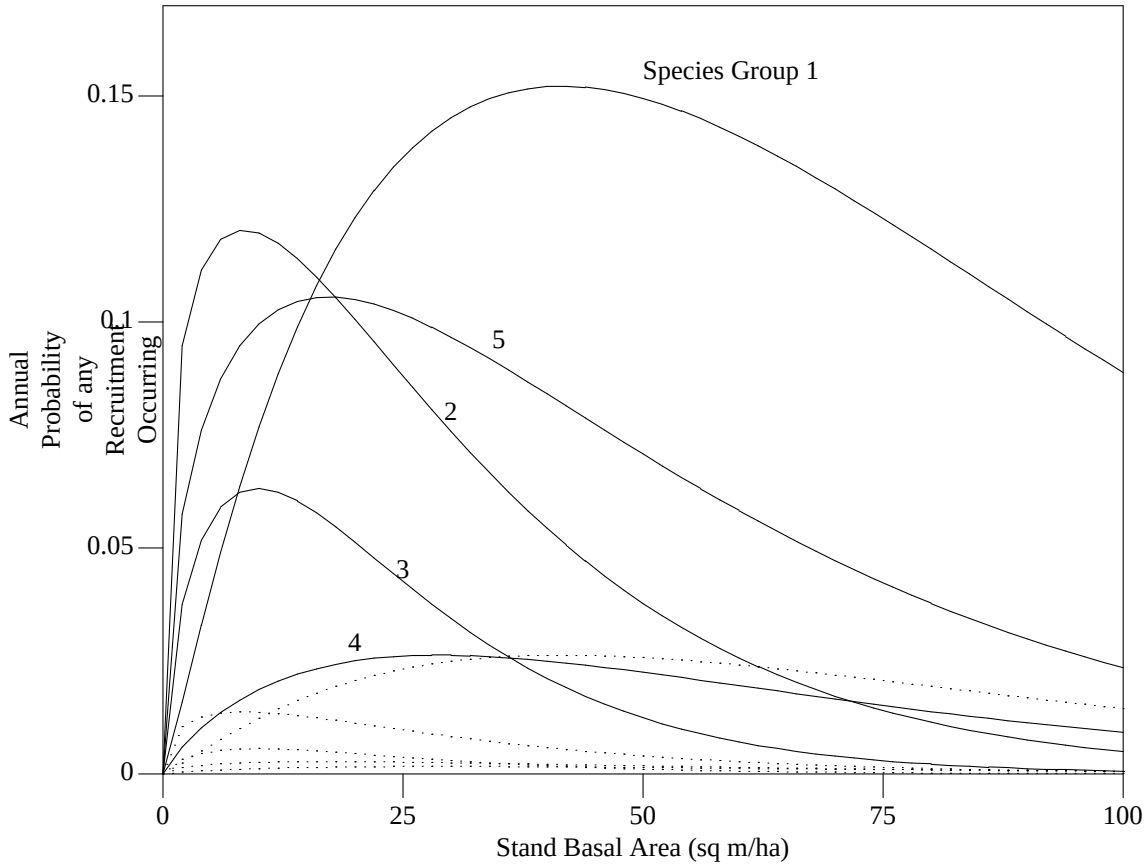

Figure 2. Predicted Probability of Recruitment
with SOIL=0, TR=0 and PRES=1 (Solid lines) or PRES=0 (Dotted)

TABLE 2. Parameter Estimates for Equation 2

Species Group	Estimate for Parameter β_0	β_1 Log(BA)	β_2 Log(RNO+.2)	β_3 SQ	β_4 SOIL
1	4.971***	–0.5460***	0.807***	0.05122***	
2	6.065***	–0.5803***	1.845***	0.09969***	–0.3166***
3	6.967***	–0.3855**	1.721***	–0.09394**	–0.3166†
4	3.150***	–0.0087	0.710***	0.02270	–0.3166†
5	4.471***	–0.2833***	1.106***	0.06213***	–0.3166†
6	5.759***	–0.7432***	0.731***	0.04963	
7	6.305***	–0.3229	1.936***	0.04943**	–0.3166†
8	3.382***	–0.3228***	0.324***	0.01440	

†These parameters are all identical to $\beta_{4,2}$
*** indicates P<0.001, ** P<0.01, * P<0.05

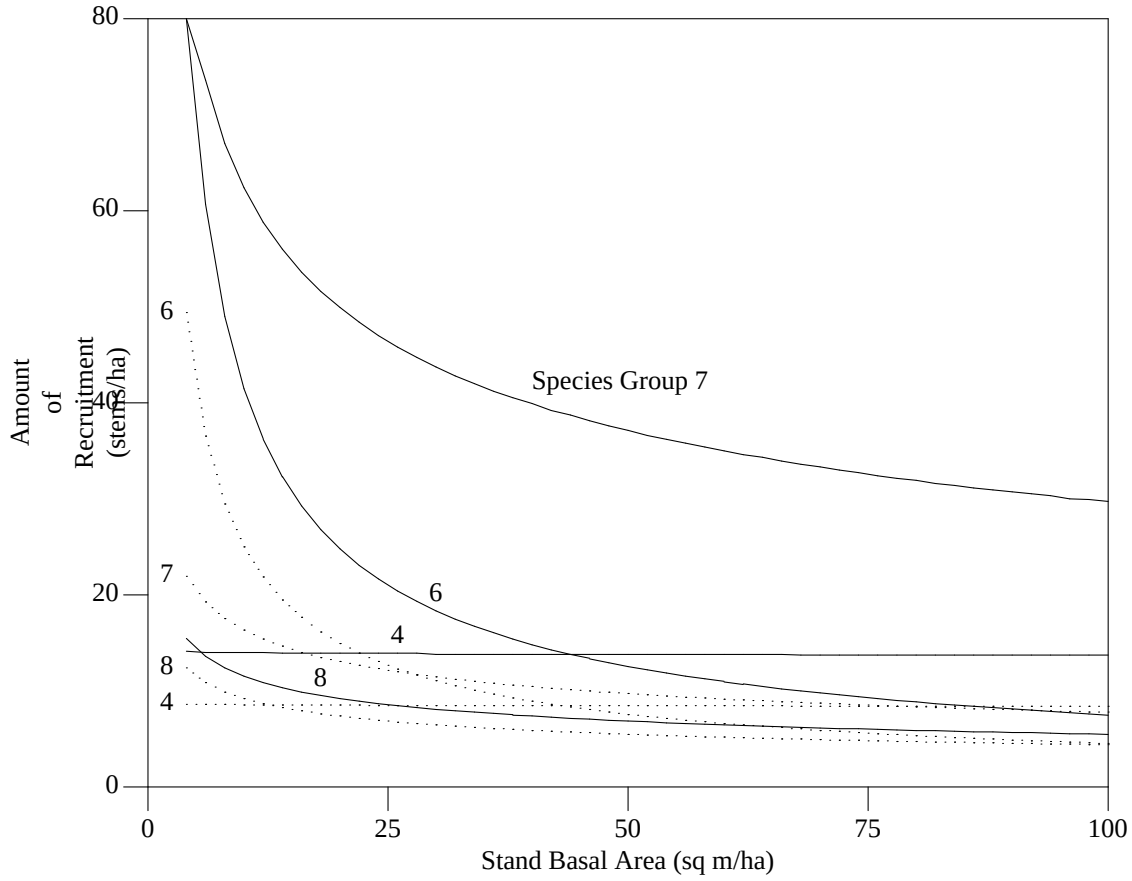

Figure 3. Predicted Amount of Recruitment, given that some occurs with SQ=7, SOIL=0 and RNO=0.2 (solid lines) or RNO=0 (dotted).

TABLE 3. Comparison of Observed and Predicted Recruitment

Group & No. of Species		Stand Basal Area (sq m/ha) 0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	Total Recruitment
1-1	O	93	885	1031	833	645	240	169	82	28	4007
(1)	P	101	1008	1514	1202	885	633	234	132	36	5745
2-2	O	1271	3648	3266	2743	810	163	30	14	747	12692
(1)	P	1441	3724	2020	1471	627	167	37	10	3	9499
2-3	O	393	2758	1852	1807	242	52	14	10	0	7128
(2)	P	431	2252	1571	1007	321	98	31	8	3	5724
2-5	O	499	2801	3655	1909	809	87	44	35	128	9967
(4)	P	1317	4480	3954	2215	958	280	65	27	11	13306
2-6	O	817	2886	2183	775	143	111	10	0	0	6925
(3)	P	814	2326	1801	745	264	130	15	12	3	6110
3-1	O	224	1132	496	248	170	7	10	0	0	2288
(5)	P	249	874	560	267	114	43	9	3	0	2118
3-2	O	104	436	203	74	20	0	0	0	0	837
(1)	P	105	232	142	44	18	6	1	0	0	549
3-4	O	149	769	607	473	105	20	2	0	0	2124
(2)	P	185	930	639	349	131	44	11	3	1	2292
3-5	O	33	113	61	0	10	0	0	0	0	217
(1)	P	100	206	119	54	20	10	3	0	0	513
3-8	O	473	1382	1041	490	182	49	5	0	0	3622
(7)	P	380	1385	1017	440	157	65	12	4	1	3461
4-1	O	49	64	46	104	35	10	10	0	0	317
(1)	P	10	52	74	61	40	13	3	6	0	259
4-2	O	82	725	749	477	230	108	89	56	27	2543
(14)	P	102	566	731	517	358	206	48	33	8	2570
4-3	O	0	0	20	147	15	0	0	5	0	187
(1)	P	9	44	38	48	52	20	6	6	1	225
4-4	O	13	373	409	329	183	91	127	48	6	1579
(5)	P	21	171	269	228	199	126	47	22	9	1091
4-5	O	78	95	230	334	312	27	25	21	6	1128
(2)	P	21	95	132	107	101	42	20	17	6	541
4-7	O	0	40	34	108	102	80	106	92	0	560
(2)	P	26	156	130	95	68	43	22	19	1	559
4-8	O	274	1485	1983	1709	995	417	144	107	19	7135
(38)	P	256	1803	2138	1730	1191	857	223	127	25	8349
5-1	O	122	350	107	40	102	22	0	0	0	743
(1)	P	74	299	204	103	66	50	26	7	0	830
5-2	O	9	222	122	76	20	34	2	0	7	493
(1)	P	19	114	171	97	100	67	12	8	4	591
5-4	O	221	988	1679	885	930	255	119	17	7	5101
(3)	P	423	1271	1442	929	667	267	69	72	10	5150
5-7	O	161	595	558	135	128	173	463	41	0	2254
(3)	P	83	447	628	337	194	148	104	51	1	1992
5-8	O	25	22	43	126	58	116	54	5	0	448
(2)	P	20	93	164	215	144	136	36	16	0	824
All	O	5091	21768	20374	13821	6244	2063	1424	533	976	72295
(100)	P	6190	22527	19457	12260	6673	3448	1033	584	124	72298
No. Cases		53	200	187	140	101	51	28	22	9	791

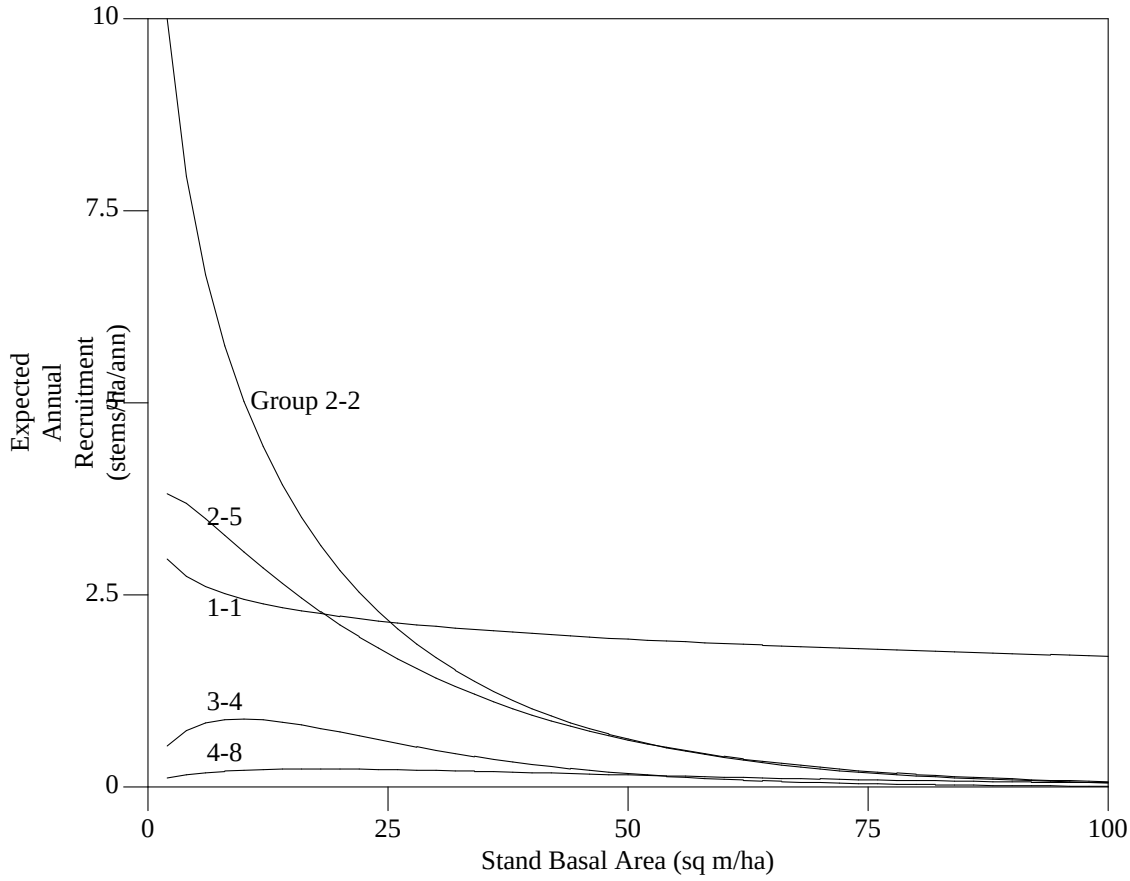

Figure 4. Expected Average Annual Recruitment for Major Species Groups
(with PRES=1, RNO=0.2, SQ=7, SOIL=0, TR=0)

TABLE 4. Species Composition of Groups

Amount of Recruitment	Groups for Predicting Probability of Recruitment					Total
	Group 1	Group 2	Group 3	Group 4	Group 5	
Group 1	MIS†		CMH,EVD,NBD NTQ,SST	NHQ	CNN	8
Group 2		MSW†	SLQ	BSH,BTD,CLL COL,FKJ,HKA PAL,QWN,RLL RSS,TBH,WBH WHZ,YEV	WAS	17
Group 3		BSL,NRA†		WAL		3
Group 4			CLO,NSO†	BKR,HYW,IBS PTM,RCD	BRT,NSS RDT	10
Group 5		ALB,BWD QMP†,QSA	ROO	LAN,SMP		7
Group 6		HMW,PKA WBS†				3
Group 7				BBN,SVB	BTM†,TYW WCD	5
Group 8			BRO,BSO,NEV PPW,SSW,TRQ WCB	NRW†,RBN† & 36 Spp.	BRY†,BUA	47
Total	1	10	16	63	10	100